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The effect of shrubs on tree recruitment differs between planted and secondary forests

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ABSTRACT

Recruitment of tree species is a bottleneck for forest regeneration, particularly in water-limited environments, such as Mediterranean forests. Despite nurse shrubs facilitating tree recruitment in adverse environments, we lack information on the facilitative role of functionally different shrubs while considering previous land uses. This study evaluates the effect of shrubs on tree recruitment in planted and secondary forests along environmental gradients, assessing how recruitment depends on the identity of shrub functional types and the beneficiary tree species. We used the Spanish Forest Inventory database to calculate tree recruitment for main tree species (pines or oaks) and shrub abundance in forests of central Spain. We fitted generalised linear mixed models of tree juvenile abundance and seedling occurrence to test the effect of shrub crown volume and forest type, considering all shrub species and the main families. Forest type (planted or secondary) modulated the relationship between shrub volume and tree juvenile abundance per species, but had a more limited effect on seedling occurrence. In some cases, planted forests reduced the effects of shrub volume on recruitment compared to secondary forests or promoted hump-shaped responses, with a peak at moderate shrub volumes. In general, juvenile abundance was less affected by shrubs than by forest type, being higher in secondary forests, especially for oak species. We also found species-specific relationships of shrub volume with tree recruitment. Occurrence of *Q. ilex* seedlings was strongly associated with various shrub families, while only one shrub family at most was related to the recruitment of the rest of tree species.

RECOMMENDATIONS

- Planted and secondary forests generate different recruitment patterns that should be considered in land use planning.
- Future restoration projects should consider the different effect of shrub families on tree recruitment to optimise forest regeneration.
- Managing both tree stand and shrub cover together can maximize tree recruitment.

1. Introduction

Tree recruitment at early forest stages determines long-term forest structure and composition (Kobe, 1996). However, establishment of tree juveniles is a bottleneck for forest colonisation and secondary succession in water-limited environments (Standish et al., 2007). For example, forest succession in Mediterranean abandoned fields resulted in *c.* 60 oak juveniles ha^{-1} after 30 years (Cruz-Alonso et al., 2020) and regeneration rates can be lower than 4 recruits ha^{-1} year^{-1} (Rey Benayas et al., 2015; Rey-Benayas et al., 2025). The importance of facilitation by nurse shrubs to overcome this bottleneck has been recognised in Mediterranean forests around the globe (Castro et al., 2004; Fleury et al., 2015; Gómez-Aparicio et al., 2005; Padilla and Pugnaire, 2009; Perea et al., 2017), but few studies have considered how species-specific

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facilitation could shape forest composition along environmental gradients and including different land use legacies across the landscape (Gómez-Aparicio et al., 2004; Plieninger et al., 2010).

Tree species colonization and establishment into new forest or non-forest patches depends on the abiotic and biotic environment of new colonized patches, which directly determines propagule pressure and resource availability (Andivia et al., 2017; Jordano et al., 2004). Abiotic factors such as summer drought are critical for forest regeneration and productivity in Mediterranean-climate regions (Andivia et al., 2017; Di Castri and Mooney, 1973; Ruiz-Benito et al., 2012; Sánchez-Gómez et al., 2006). The negative consequences of summer drought on plant performance can be aggravated in low water-retention soils (Ibáñez et al., 2014).

Biotic factors such as plant interactions modulate the effect of the abiotic environment on tree establishment (e.g. Navarro-Cano et al., 2016). In fact, facilitation by nurse shrubs can alleviate water and heat stress of the beneficiary tree seedlings (Gómez-Aparicio et al., 2004), while competition with adult trees can aggravate the stress of juveniles (Caldeira et al., 2014; Prévosto et al., 2012). The balance along the continuum of positive (facilitative) and negative (competitive) shrub-tree and tree-tree interactions (Holmgren et al., 1997) has direct implications on tree recruitment, and understanding which environmental conditions and plant ontogenetic stage favour facilitation vs. competition can inform forest restoration projects (e.g., Castro et al., 2004).

The net outcome of facilitative and competitive interactions depends on the functional identity of the interacting plant species (Verdú et al., 2012). The facilitative effect of shrubs has been related to specific functional attributes such as canopy size (Navarro-Cano et al., 2016), defences against herbivory (Perea and Gil, 2014), root intensity and distribution (Navarro-Cano et al., 2018; Rolo et al., 2013), and not producing allelopathic compounds (Chaves et al., 2001). Tree seedlings with low water-stress tolerance and high palatability might especially benefit from nurse plants through amelioration of harsh abiotic conditions and protection against herbivory (Gómez-Aparicio et al., 2008; Liancourt et al., 2005). In this regard, pines (*Pinus* spp.) and oaks (*Quercus* spp.), dominant tree species in the forests of the Mediterranean basin (Costa et al., 2005), have regeneration niches markedly different (Vayreda et al., 2013; Zavala et al., 2011). Mediterranean pines are anemochorous, shade-intolerant, and drought-avoiders (*sensu* Levitt 1980, i.e., they maintain high water potential by closing their stomata with water stress), while oaks are zoochorous and more shade- and drought-tolerant (i.e., they maintain high transpiration and photosynthetic rates even when plant water potential is low; Carnicer et al., 2013). In addition, the high concentration of phenolic compounds and resins and the sharp needles make pines less palatable than oaks (Baraza et al., 2006).

Different land uses have led to forests with different structure and composition that may shift the nurse role of understory shrubs for tree recruitment (Prévosto et al., 2012; Ruiz-Benito et al., 2012). Planted forests usually show even-aged structures with high tree density and canopy cover. In fact, many of the current dense and monospecific pine stands in the Mediterranean basin are the result of forest plantation initiatives during the 20th century (Sheffer, 2012; Vadell et al., 2016). In contrast, secondary forests developed after the cessation of agricultural use show more heterogeneous structure in terms of tree size and species richness (Cruz-Alonso et al., 2019). Shrubs can act as nurse plants in planted forests for new seedlings by protecting juveniles from herbivory (Gavinet et al., 2016) or attracting seed dispersers (Pérez-Camacho et al., 2023). However, the facilitative effect of shrubs by reducing light and water stress of beneficiary plants might be reduced or shifted to competition under the shade of overstory trees (Douaihy et al., 2022; Prévosto et al., 2012). In addition, shrub communities can be less abundant in planted forests (Dagan and Izhaki, 2019; Maestre and Cortina, 2004; Nichol and Abbas, 2021; Vu Ho et al., 2023), reducing both the facilitative capacity of nurse shrubs and the negative effect of highly competitive shrubs that become less abundant (i.e. indirect facilitation, Cuesta et al., 2010). Reforestation constitutes *c.* 23 % of total forest area expansion between 1990 and 2010 in the Mediterranean basin, and secondary forests growing in old fields *c.* 67 % (FAO and Plan Bleu, 2018). However, although legacy effects of land use may modulate facilitative interactions (Prévosto et al., 2012), such linkages have mostly been explored at local scales. Examining regional-scale historical land use effects on forest composition demonstrate that land use legacies can shape forest composition and thus plant-plant interactions across broader spatial extents (Rhemtulla et al., 2009). These findings suggest that legacy-mediated facilitation might also operate beyond local contexts.

The main objective of this study was to evaluate the role of shrubs on tree recruitment of important and functionally distinct tree species from genus *Pinus* and *Quercus* widely distributed in the western Mediterranean Basin, under two contrasting land use scenarios that lead to two contrasting forest types: the establishment of planted forests (mostly pine plantations) and the colonization of old agricultural fields (hereafter, planted and secondary forests, respectively), along broad aridity and soil gradients. Specifically, we aimed to (1) quantify the relationship between shrub abundance and tree recruitment in each forest type in central Spain, considering consolidated and recently-established tree recruits; and (2) assess if the relationship between shrub abundance and tree recruitment depends on the identity of shrub functional types and the beneficiary tree species (i.e., *Pinus sylvestris, Pinus pinea, Pinus pinaster, Quercus pyrenaica* and *Quercus ilex*).

We hypothesised that the recruitment patterns related to tree competition in planted forests offset the facilitative and competitive effect of nurse shrubs on tree regeneration, but that these relationships are strongly modulated by the functional identity of shrubs and beneficiary trees. According to the contrasting functional strategies of pines and oaks, we expect that nurse shrubs (i.e. those alleviating water stress and protecting against herbivory) benefit more oaks than pines when recruited under their canopies. We distinguished between all and recently-established recruits because patterns of consolidated recruits (hereafter tree juveniles) would result from processes and factors operating along many years, whereas drivers of recently-established recruits (seedlings) would operate over shorter periods. Our results can help to design future forest restoration projects and silviculture practices to enhance facilitative interactions between specific tree and shrub species, as well as provide new insights into the ecological theory of facilitative and competitive interactions.

2. Materials and methods

2.1. Study area

The study area encompasses the Community of Madrid, which covers *c.* 8000 km^2 in central Spain (Figure S1). Climate is continental Mediterranean, with mean annual temperature and annual rainfall between 7 and 15 ºC and 400 and 2000 mm, respectively (CAM, 2007). In the region, there is a transition from *Pinus sylvestris* L. forests at the highest (1500–1900 m a.s.l.) and coldest and wettest sites to *Quercus ilex* L. forests in the lowest elevations (500–1000 m a.s.l.) and warmest and driest sites. The intermediate altitude and precipitation sites, where primary productivity peaks, are dominated by *Quercus pyrenaica* Willd. forests. *Quercus faginea* Lamk. and *Pinus nigra* Am. are also present in mid-altitude sites. In addition, mixed forests of the Mediterranean pines *Pinus pinea* L. and *Pinus pinaster* Aiton occupy the South-West area at 550–1650 m a.s.l. Soils have contrasting chemical composition ranging from alkaline, which mostly come from limestones and casts, in the southeast to acid entisols and inceptisols originated from granites and gneisses in the rest of the region (Rodríguez-Rastrero et al., 1991). As forest plant communities can differ between soil types and forests are scarce in the southeast area of the study region (CAM, 2007), we excluded alkaline soils from our analysis.

2.2. Forest inventory data

We used the Spanish Forest Inventory (SFI hereafter; Alberdi et al., 2016; Vallejo and Sandoval, 2013) to evaluate shrub composition and tree recruitment in the Madrid region in 2000 (3rd SFI) and 2012–2013 (4th SFI). The SFI is a systematic network of permanent plots on forests and scrublands (initial forest cover > 5 %) at a density of 1 plot per km^2. We selected periodically surveyed plots with (1) at least one alive tree, recruit or shrub, (2) no presence of planted juveniles, and (3) less than 25 % of stand basal area corresponding to riparian species (i.e. *Alnus glutinosa* (L.) Gaertn., *Fraxinus angustifolia* Vahl, *Populus* sp., *Salix* sp. and *Tamarix* sp.).

Each SFI plot has four concentric circular subplots of 5, 10, 15 and 25-m radius. An adult tree is sampled in the 5 m-radius subplot if its height is > 130 cm and its diameter at breast height (d.b.h.) is 7.5–12.4 cm; if d.b.h. is 12.5–22.4 cm, the tree is sampled in the 10 m-radius subplot; if d.b.h. is 22.5–42.4 cm, in the 15 m-radius subplot; and if d.b.h. ≥ 42.5 cm, it is sampled in the 25-m radius subplot. Adult trees are identified and classified as alive or dead, and the height and d.b.h. are recorded for each tree alive. Shrub cover (%) and mean height (dm) of each shrub species or taxonomic group are sampled in the 10-m radius subplots, and recruitment (i.e. trees with d.b.h. < 7.5 cm or height < 130 cm) is measured in the 5-m radius subplots.

In the SFI, tree recruitment is recorded by species differentiating four size categories according to the height and d.b.h. of the juveniles. For the first three size categories (1: height < 30 cm; 2: height 30–130 cm; 3: height > 130 cm and d.b.h. < 2.5 cm), abundance is recorded using a semi-quantitative scale (scarce: 1–4 recruits; intermediate: 5–15; abundant: > 15). We transformed these data into a continuous scale, using the minimum number of juveniles in each category (i.e. 1, 5 and 16) as a conservative approach (Ruiz-Benito et al., 2012). For juveniles with height > 130 cm and d.b.h. between 2.5 and 7.5 cm (4th size category), the exact number of individuals is recorded in the SFI.

We assessed recruitment using two metrics focusing on all juveniles (the four juvenile categories together, i.e. trees of d.b.h. < 7.5 cm or height < 130 cm) and only seedlings (first size category, i.e. tree height < 30 cm). First, we calculated the density of all juveniles of all tree species (juvenile abundance) and of the main *Pinus* and *Quercus* species (i.e., *Pinus sylvestris*, *P. pinaster* and *P. pinea*, and *Quercus pyrenaica*, and *Q. ilex*) as the sum of juveniles of the four size categories. Secondly, we focused only on the occurrence of the youngest juveniles, which we assumed to be mostly seedlings (hereafter seedling occurrence). Because of the semi-quantitative scale for measuring recruitment abundance in the SFI, when the metric was calculated with only one size category (i.e., seedlings), we found sounder to study the process of occurrence instead of quantifying abundance.

2.3. Explanatory variables of tree recruitment

We used eight potential predictors of tree recruitment estimated for each SFI plot: (1) forest type (planted and secondary forests), (2) forest age (No. years), (3) altitude (m a.s.l.), (4) SFI survey, (5) maximum slope (degrees), (6) tree basal area (m^2 ha^{-1}), (7) forest cover (%), and (8) shrub crown volume (hereafter shrub volume, m^3). We classified each plot as planted or secondary forest and calculated forest age by photo-interpretation of aerial images at the coordinates of the SFI plots and analysis of the sequence of past land cover types on eight temporal points from 1933 to 2009. We estimated forest age based on the year the plot was abandoned or planted. The abandonment or plantation year was set as the central year of the period when the shift from agricultural field to shrubland or forest was observed (see Cruz-Alonso et al., 2019 for the methodological details). Altitude was used as a surrogate of mean temperature and annual precipitation in the study area (Pearson's correlation considering all data of −0.98 and 0.93, respectively). We extracted altitude from a digital elevation model of 50-cm resolution (IGN, 2009) with ArcMap 10.0 (ESRI Inc., Redlands, CA, USA) using the coordinates of each plot. Under Mediterranean climate conditions, interannual climate variability can influence seedling recruitment. Years with extreme drought or anomalously high rainfall may strongly diminish or enhance seedling abundance (Cruz-Alonso et al., 2020; Giorgi and Lionello, 2008; Kouba et al., 2012). As we are using two SFI surveys sampled in different years (3rd SFI in spring 2000 and 4th SFI mostly in summer 2012-winter 2013), we have included survey id in our models to account for the variability in seedling response across years. Maximum slope was obtained from SFI field data. We used maximum slope as a proxy of soil erodibility and soil depth (Martz, 1992). Deep soils store water in deeper layers that can be used by plants during the dry seasons (Tromp-van Meerveld and McDonnell, 2006). Tree basal area per plot was the sum of basal area of all alive adult trees calculated with the d.b.h. from the SFI. While stand basal area is not a direct measure of competition *per se*, it has been broadly used as a proxy for resource use of a stand, and thus resource limitation (e.g., Benavides et al., 2016; Searle et al., 2022). Forest cover was used as a surrogate of propagule pressure at a landscape scale (Andivia et al., 2017). It was calculated as the percentage of forest and shrubland in a 1-km-radius area around the plot centre over the Spanish Forest Map contemporary to the different SFI surveys (Table S1), using ArcMap 10.0 (ESRI Inc., Redlands, CA, USA).

We calculated the shrub volume per taxa as the product of shrub cover and mean height from the SFI. Then, we summed up the volume by plot (hereafter, all shrub volume) and by family. For shrub families, we classified the species and species groups into taxonomic families (Table S2) and analysed the seven most abundant families (see below *Datasets for linking tree recruitment to shrub presence*). We removed five wrong shrub volume measurements because of heights > 3 m and cover per taxa > 100 %, and one extreme volume value of 800 m^3 $plot^{-1}$. We assumed that shrub families represent functional types with more similar facilitative and competitive capacities than with other families (Verdú et al., 2012; see supplementary section *Linking shrub families with functional traits related to facilitative ability*).

2.4. Datasets for linking tree recruitment to shrub presence

First, a complete dataset with recruitment of all tree species and all shrub volume summed up in the selected SFI plots was used for the analysis. For a detailed analysis, to explore (1) the relationships of recruitment of each tree species and total shrub volume, and (2) the relationships of the different shrub families and total tree recruitment, we considered those SFI plots within the distribution areas of each of the main tree species for (1) (Figures S2), and we considered SFI plots within the distribution areas of the shrub families for (2) (Figures S3). We defined distribution areas for seven tree species and eleven shrub families in two steps (Table S4). First, we delimited the geographical areas where the tree juveniles or the shrubs were recorded either in the 3rd or 4th SFI surveys using minimum convex polygons. Secondly, we restricted the polygons to the altitudinal gradient (i.e., climatic conditions; from 0.025 to 0.975 percentiles) where the species was present (Figures S2 and S3). Plots without tree recruitment or shrubs within each final restricted polygon were considered as absences (i.e., abundance equals zero) for each tree species and shrub family, enabling us to minimise absences out of recruitment area and zeros in the analysis. We discarded further analysis with *Pinus nigra* because of the low number of plots in the distribution area, and with *Quercus faginea* because of the low number of plots with tree recruitment (Table S4).

To analyse the effect of the different shrub families on the recruitment of each tree species separately, we considered those SFI plots within the distribution areas where each of the main tree species (Figures S2) and shrub families (Figures S3) could potentially regenerate and grow together. For the analysis we checked the SFI plots within the overlap of the distribution area of each tree species and each shrub family. We further analysed specific tree species-shrub family combinations when the following criteria were fulfilled: (1) there were at least

160 observations –since we estimated 16 parameters per model at most and it is recommended to have ten observations per parameter for conservative calculations (Crawley, 2015)- in the overlap of specific combinations of tree species-shrub family distribution areas; (2) the tree species and the shrub family co-occurred in at least 10 % of the plots for planted forests and 10 % of the plots of secondary forests separately –since we wanted to test the differences on the parameters of the shrub families in each forest type (Table S4, Figure S5, Figure S6). As a result, we could test the effect of seven shrub families (*Asparagaceae, Asteraceae, Cistaceae, Ericaceae, Labiatae, Leguminosae, Rosaceae, Thymelaeaceae*) on the recruitment of some of the following three tree species: *Quercus ilex* (evergreen broad-leaved), *Q. pyrenaica* (deciduous broad-leaved), and *P. pinea* (evergreen needle-leaved), resulting in the analysis of the most common 10 tree species-shrub family combinations (Table S4, Figure S6).

2.5. Statistical analyses

We used generalised linear mixed models to test the shrub relationship with tree recruitment (juvenile abundance and seedling occurrence) in the planted and secondary forests. We fitted models with the total shrub volume and, then, fitted separated models per shrub family. Additionally, we tested the shrub relationship (total volume and per family) with the abundance of juveniles of each tree species separately and on the presence of seedlings of each tree species. We used the package *glmmTMB* (Brooks et al., 2017) in R 4.4.2 (R Core Team, 2024). The juveniles abundance was modelled using a Poisson distribution with a log link function, but in cases where data were overdispersed we used a negative binomial distribution with a log link function in which variance increased linearly with the mean (total and *Q. ilex* juveniles; Brooks et al., 2017; Zuur et al., 2013). We removed three and one outliers in total and *Q. ilex* juveniles models with > 3.5 and > 4 Pearson residuals, respectively, that were clearly separated from other observations. The seedling occurrence was modelled using a binomial distribution with a logit link function.

Plot identity was considered as a random effect to account for non-independence due to successive surveys in the same plots. As fixed effects, we considered the forest type (i.e. planted or secondary forest), shrub volume, and the forest type × shrub volume interaction, and forest age, altitude, survey, maximum slope, tree basal area and forest cover around each plot as covariates. We included altitude and tree basal area as quadratic covariates because recruitment can peak at intermediate levels of these variables (Benavides et al., 2016; Ruiz-Benito et al., 2012). By including quadratic forms we allow hump-shaped non-linear responses, but also monotonic responses within constrained ranges along axes. We included shrub volume as a quadratic and linear variable and checked which option better adjusted to the data according to the minimum Akaike Information Criterion corrected for small samples (AICc; Burnham and Anderson, 2002) and the parsimony principle (Tables S5 and S6). All numerical predictor variables were standardised (Schielzeth, 2010) and low collinearity was checked using VIF tests (Dormann et al., 2013).

To test if forest type and the shrub volume affected tree recruitment and whether the effect of the shrub volume differed between the two forest types (objective 1), we compared the full model with models where the interaction forest type × shrub volume and the main effects were dropped from the full model in three steps. First, we compared the full model with a model where the interaction term "forest type × shrub volume" was dropped ("No interaction"). Then, if the model without interaction was supported, it was compared to a model without forest type ("No forest type") and to a model without shrub volume ("No shrub volume"). Finally, in cases where one of these variables was supported in the best model, the models were compared with a simpler one where both variables were dropped ("No forest type & no shrub volume"). We repeated the comparisons for models with the volume of all shrub species together and the volume of each shrub family and for models where the response variables related to all tree recruited species or to specific tree species (pines or oaks; objective 2). The comparisons were based in the AIC, using a $\Delta AIC > 2$ for supporting the most complex model (Burnham and Anderson, 2002).

3. Results

3.1. Effect of forest type and shrub volume on tree recruitment

The effect of forest type (i.e., planted or secondary) or its interaction with shrub volume on recruitment was especially supported in best models when juvenile abundance was considered, compared to seedling occurrence (Tables S7 and S10). For juveniles, recruitment was more abundant in secondary than in planted forests, especially due to *Quercus* spp. (Fig 1a and 1b; Tables S7a and S8). Forest type conditioned the relationship that shrub volume had with juvenile abundance, i.e. the interaction forest type × shrub volume was supported for total shrub volume in *P. sylvestris* and *P. pinea* models, and for *Rosaceae* shrub volume in *Q. pyrenaica* and *Q. ilex* models (see Section 3.2. *Specific responses of tree recruitment to shrub volume of different families* for further details; Tables S10a and S11).

Seedling occurrence was mostly independent of forest type (Fig 1c and 1d; Tables S7b and S9), but forest type modulated the relationship of *Asteraceae* and *Leguminosae* shrub volume with the probability of total and *Q. ilex* seedling occurrence (see Section 3.2. *Specific responses of tree recruitment to shrub volume of different families for further details*; Tables S10b and S12). Forest type also had an effect on the occurrence probability of *Q. pyrenaica* seedlings, independently of shrub volume, being higher in secondary than in planted forests (Tables S10b and S12).

The relationships of shrub volume and recruitment varied according to the recruit life stage (juvenile or seedling) and the analysed tree species. Total shrub volume was significantly related to juvenile abundance of all tree species except for *Q. ilex* (Fig. 2a), and juvenile abundance increased with shrub volume for *P. pinaster* and *Q. pyrenaica* (Tables S10a and S10b). Total shrub volume was negatively associated with the probability of total seedling occurrence, and especially of *Quercus* spp. (Fig. 2b, Table S10b and Table S12).

When forest type modulated the relationship of shrub volume with juvenile abundance (i.e., the interaction forest type × shrub volume was supported in the best model), we found that a peak of juvenile abundance occurred at low shrub volumes and then decreased to minimum values in planted forests (Fig. 2a). Specifically, the abundance of *Pinus* spp. juveniles peaked at *c.* 100 m^3 shrub volume compared to secondary forests, and higher shrub volumes were associated with decreasing juvenile abundance in planted forests. When tree recruitment exhibited a humped response to shrub volume, the shrub volume that maximized recruitment was substantially higher in secondary forests than in planted ones (e.g., *P. pinea* juvenile abundance; Fig. 2a).

3.2. Specific responses of tree recruitment to different shrub families

Total juvenile abundance when all tree species are considered together was not significantly related to any of the seven shrub families (Table S7a and Table S10a). However, the probability of seedling occurrence was positively related to the volume of *Asparagaceae*, the volume of *Asteraceae* in secondary forests and the volume of *Leguminosae* in planted forests, and negatively to the volume of *Rosaceae* (Table S7a and Table S10a, Fig. 4). In general, juvenile abundance of each tree species was related to shrub volume independently of the shrub family, while the probability of seedling occurrence had different relationships to shrub volume depending on shrub families.

We only found three species-specific relationships for juvenile abundance (Fig. 3). The relationships between the abundance of *P. pinea* juveniles and the *Labiatae* volume and between the abundance of *Q. pyrenaica* juveniles and the *Rosaceae* volume in planted forests were humpbacked (Fig. 3). Instead, the abundance of *Q. pyrenaica* juveniles

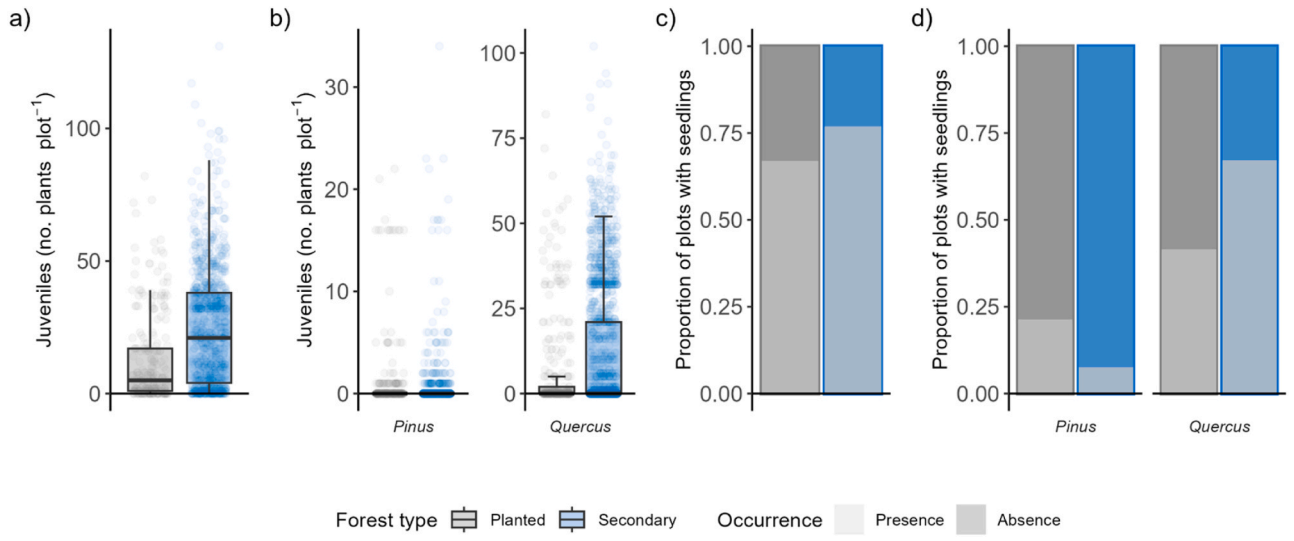

Fig. 1. Tree recruitment in planted and secondary forests: (a) boxplots for juvenile abundance, (b) boxplots for juvenile abundance by genus, i.e., *Pinus* and *Quercus*., (c) seedling occurrence, and (d) seedling occurrence by genus. See Fig. S7 for juvenile abundance by tree species and volume of shrub families. Dots over the boxplots represent the original data.

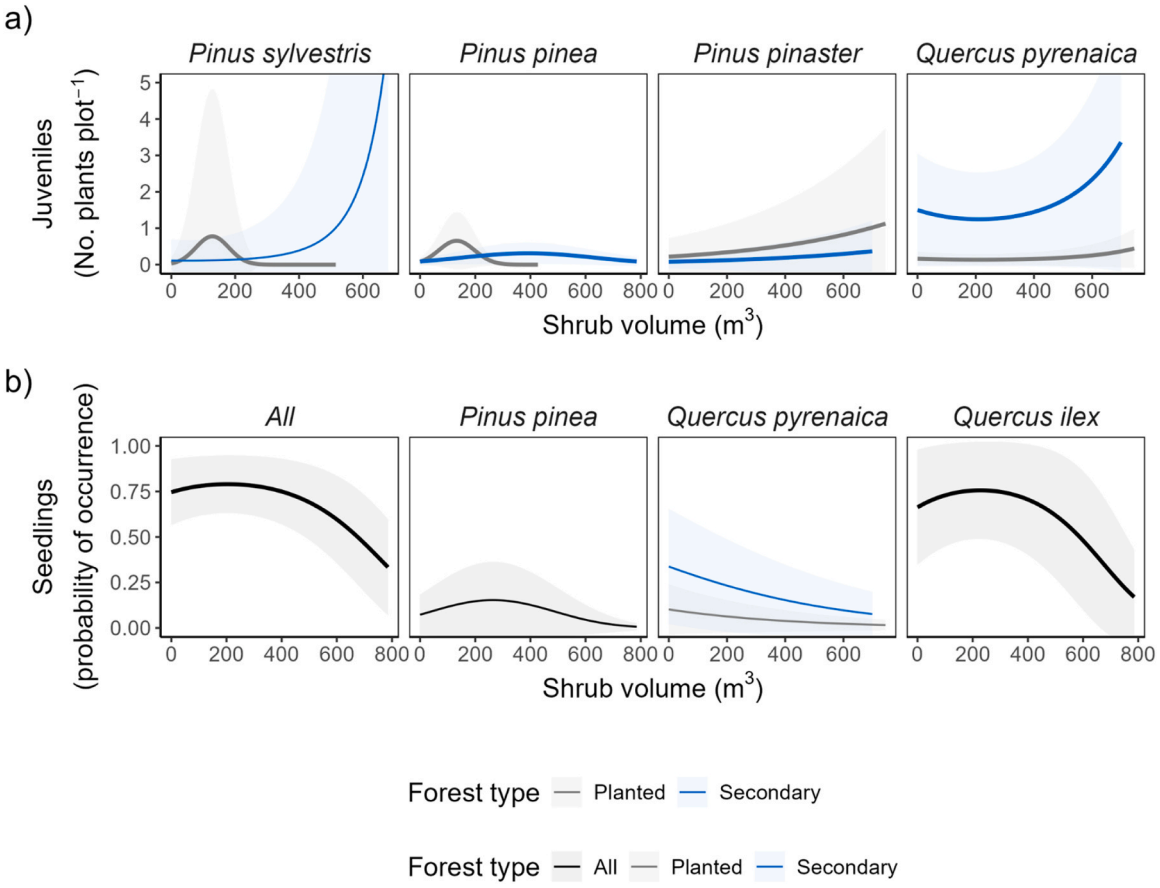

Fig. 2. Predicted juvenile abundance (a) and probability of seedling occurrence (b) in relation to total shrub volume when the effect of shrub volume was supported in the best model (Table S7) for the main tree species present in the Community of Madrid either depending on forest type (planted and secondary forests shown in grey and blue lines) or not (black lines). Effects different from zero (i.e. with p-value < 0.05) are shown with thicker lines. Note that the comparison of juvenile abundance and seedling occurrence between planted and secondary forests could be only performed for the range of shrub volume available for both, but the graphical representation ranges between the minimum and maximum shrub volume values for each forest type.

increased with *Rosaceae* volume and the abundance of *Q. ilex* juveniles decreased in secondary forests (Fig. 3).

Among all tree species, the occurrence of *Q. ilex* seedlings was the only related to all shrub families (*Asparagaceae, Asteraceae, Cistaceae, Leguminosae, Rosaceae* and *Thymelaeaceae*) except *Labiatae* (Tables S10b and Table S12, Fig. 4). Regardless of forest type, models predicted a

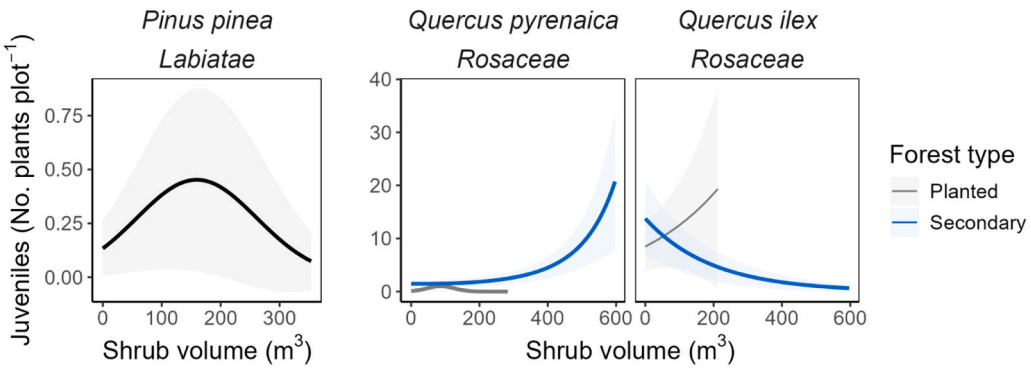

Fig. 3. Predicted juvenile abundance with shrub volume per family when its effect was supported in the best model (Table S10a), either depending on forest type (planted and secondary forests shown in grey and blue) or not (black lines). Effects different from zero (i.e. with p-value < 0.05) are shown with thicker lines. Note that the comparison of seedling abundance between planted and secondary forests could be only performed for the range of shrub volume available for both, and that the horizontal axis has been limited to 300 m^3 of shrub volume to facilitate comparisons.

lower probability of *Q. ilex* seedling occurrence with high values of shrub volume except for *Asparagaceae* and for *Leguminosae* in planted forests, and a maximum probability of occurrence with small to moderate volume values for *Asteraceae*, *Cistaceae, Rosaceae* and *Thymelaeaceae* (Fig. 4, Table S10b and Table S12).

4. Discussion

This study evaluated the role of shrubs on tree recruitment under two contrasting forest types that originated from different land uses (i.e., planted and secondary forests) along broad climatic and edaphic gradients in Mediterranean environments. We evidenced that shrub abundance related to tree recruitment and assessed how functionally distinct shrubs modulated the recruitment of ecologically different tree species. Overall, as we hypothesised, there were cases when in planted forests, the relationship between shrub volume and recruitment was less positive or there was a peak on recruitment at moderate levels of shrub volume compared to secondary forests. This suggests that competition in planted forests may be able to offset the facilitative or competitive effect of nurse shrubs, which is more evident in secondary forests. The recruitment response to shrub abundance depended on the tree species and the shrub family analysed pointing to the role of functional identity on plant-plant interactions.

4.1. Why does forest type affect tree recruitment?

Forest type, i.e. planted or secondary forest, modulated the relationship between shrub volume and juvenile abundance of *Quercus* and *Pinus* species, but was hardly related to seedling occurrence. In addition, juvenile abundance was greater in secondary than in planted forests, especially for oak species. The observed patterns can be explained by differences in the time-scale of the recruitment processes between the abundance of juveniles and the occurrence of seedlings, and the factors driving them. In the study area, both forest types have contrasting structural characteristics that generally lead to higher tree competition in planted than in secondary forests (Cruz-Alonso et al., 2019), which might inhibit the establishment of juveniles over time (Gómez-Aparicio, 2009; Prévosto et al., 2012; Tíscar Oliver, 2015), but not hinder seedling emergence, especially of the large seeded *Quercus* species (Vieco Martínez et al., 2023). Our models included tree basal area to account for the effect of the adult competition on tree recruitment, which on average was more than twice in planted than in secondary forests (22.3 ± 17.0 vs. 8.6 ± 10.1 m^2 ha^{-1}, respectively); however, other stand structural characteristics might have been captured by the forest type. For example, the higher tree density, lower structural heterogeneity, more simple species composition and lower functional dispersion in planted than in secondary forests in the study area could have increased competition intensity and decreased tree establishment in the understory (Coll et al., 2011; Cruz-Alonso et al., 2019; Tíscar Oliver, 2015; Valladares and Guzmán, 2006).

The fact that the probability of seedling occurrence was similar in planted and secondary forests can be explained differently for pines and oaks. Most planted forests in Spain are dominated by pines (Vadell et al., 2016) that may result in high pine seed availability and offset the negative effect of tree competition on seedlings. For *Quercus* species, tree trunks in planted forests are attractors of acorn dispersers (Gómez, 2003). In fact, in sites where pines and oaks coexist as adults, oak seedlings are more likely to occur than pine seedlings, which suggest a stronger indirect facilitative effect on oak early establishment of adult trees in planted stands (Carnicer et al., 2014; Ruiz-Benito et al., 2012; Urbieta et al., 2011). Also, we found a higher abundance of *Leguminosae* shrubs in secondary than planted forests (Figure S7c), that have been suggested as key nurse shrubs in Mediterranean environments (Gómez-Aparicio et al., 2004; Perea and Gil, 2014; Pugnaire et al., 1996) and, therefore, could have contributed to balance seedling occurrence in both forest types. Main leguminous species in the study area, besides fixing atmospheric N and enrich soil nutrient conditions in their surroundings, were related to facilitative traits as having spinose tissues, and not generating allelopathic compounds, and had relatively resource-conservative life strategies (Figure S2).

An exception to the similar seedling occurrence in planted and secondary forests was found for the mesic *Q. pyrenaica,* with a higher occurrence in secondary than in planted forests (Table S12d). As this pattern was not observed in the xeric *Q. ilex,* it might suggest a greater benefit of nurse shrubs on *Q. pyrenaica* than *Q. ilex* likely due to its lower stress tolerance (Gil-Pelegrín et al., 2017) or higher palatability (Costa et al., 2017; Mediavilla et al., 2018) than *Q. ilex*. Importantly, herbivory pressure, which was not included in our models, could also contribute to these species-specific differences since the frequency of the positive relationships between oak recruitment abundance and shrub cover is expected to increase with herbivore abundance according to the Stress Gradient Hypothesis (Bertness and Callaway, 1994).

Forest type also affected tree recruitment by modulating the effect of shrub volume. We observed differential relationships between shrub volume and recruitment in planted and secondary forests in most target tree species, either for juveniles or seedlings. In planted forests, a low to moderate shrub cover was associated to a maximum on tree recruitment that could be due to attraction of seed dispersers, protection against herbivory or soil fertility improvement (Gavinet et al., 2016; Pérez-Camacho et al., 2023; Plieninger et al., 2010). Enhancement of soil fertility could be especially important in degraded soils (Gavinet et al., 2016) where planted forests were generally located (Ruiz-Benito et al., 2012; Reid et al., 2018). However, our results would agree with a shift of shrub facilitation into competition with a relatively high shrub

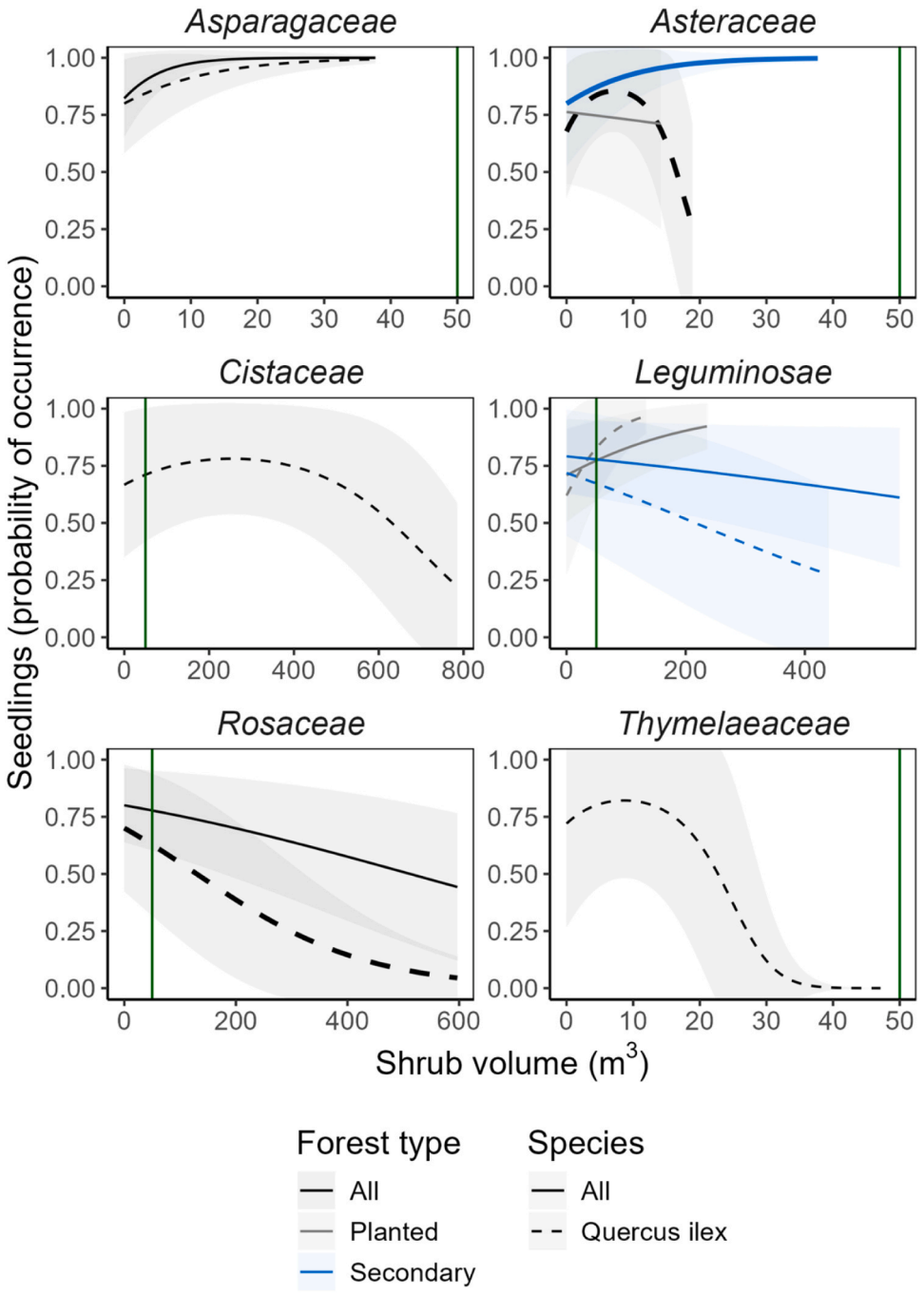

Fig. 4. Predicted probability of seedling occurrence of all tree species and of *Quercus ilex* with total or per family shrub volume when the effect shrub volume was supported in the best models (Table S10b). The effect of shrub volume is represented either interacting with forest type (planted and secondary forests shown in grey and blue, respectively) or not (black lines). Effects with p-value < 0.05 are shown with thicker lines. Green vertical lines mark 50 m^3 of shrub volume to point differences in ranges of the horizontal axis. Note that the comparison of seedling abundance between planted and secondary forests could be only performed for the range of shrub volume available for both, but the graphical representation ranges between the minimum and maximum shrub volume values for each forest type.

volume combined with a dense tree layer. Under these conditions of less water or nutrients available for every plant, mechanisms such as root competition for soil resources, can likely increase stress on tree juveniles (Maestre et al., 2009).

4.2. Tree recruitment patterns differ between pines and oaks

We observed that tree recruitment in the study area was dominated by *Q. ilex,* while the recruitment of pine species was surprisingly low (both for seedling occurrence and for juvenile abundance; Fig. 1). Consistently, Gómez-Aparicio (2009) found that pine forests can facilitate the recruitment of hardwood species and other studies found a lower recruitment of most Iberian pine species than of *Q. ilex* in stands with adult pines (Carnicer et al., 2014; Vayreda et al., 2013).

The limited recruitment of pines could be due to their lower shade-tolerance, and gap dynamics might be critical for sapling survival in comparison to more shade-tolerant species such as *Q. ilex* (Zavala et al., 2011). Further, the dispersal of pines could be more affected by forest fragmentation than the dispersal of oaks (Montoya et al., 2008), while acorns can be preferably dispersed into the pine forests such as most

plantations in the area (Gómez, 2003). The fact that part of current pine forests are outside of their natural range after extensive afforestation in the 20th century may also explain the lower recruitment of pine than oak species (Ruiz-Benito et al., 2012; Vilà-Cabrera et al. 2023). However, it is important to note that the data has limitations for species comparisons, particularly because we might be underestimating the abundance of juveniles due to the conservative approach used in calculations, especially when recruits were classified as "abundant" (see 2.2. *Forest inventory data*), which might differently affect each species.

Moderate shrub abundance could be specially beneficial for the recruitment of *P. sylvestris* and *P. pinea* as our results showed that the highest recruitment occurred at intermediate levels of shrub volumes. These results are partially in consonance with other studies showing that pine recruitment is positively related to moderate shrub cover (< 50 %) and negatively related to dense shrub encroachment (Batllori et al., 2009; Benavides et al., 2016). Also, a possible facilitative effect of *Labiatae* on *P. pinea* was observed but not for oaks (in consonance with Plieninger et al., 2010). Relatively mid to low height of *Labiatae* shrubs in the study area (Figure S2) could weakly buffer microclimate in the vicinity in comparison to larger shrubs (Navarro-Cano et al., 2016), which might be enough for facilitating the survival of the shade intolerant *P. pinea*, but not other more shade-tolerant species.

4.3. Tree species respond differently to shrub functional types

We found species-specific effects of shrub volume on tree recruitment, indicating that not all tree species benefit from shrubs. The species-specific associations could be driven by a differential modification of aboveground abiotic conditions, such as light availability and temperature; belowground environment, such as soil compaction, temperature, water content and soil fertility (Navarro-Cano et al., 2018, 2016); and biotic interactions mediated by shrub volume, such as seed dispersal, grass suppression or herbivory (Cruz-Alonso et al., 2020; Cuesta et al., 2010; Perea and Gil, 2014; Pérez-Camacho et al., 2023).

Notably, the relationship between shrub volume and juvenile abundance was different between mesic and xeric environments. For example, small volumes of spiny *Rosaceae* shrubs that can protect small trees from herbivores (Perea and Gil, 2014) were associated with a peak on the recruitment of the mesic *Q. pyrenaica* in planted forests, but a negative relationship was found for the xeric *Q. ilex*, for juveniles in secondary forests (Fig. 3) and seedlings in all forests (Fig. 4). The more limitant environment where *Q. ilex* grows with intense summer drought, could increase the competitive interactions with this family of shrubs even when they have facilitative traits such as spines and big sizes (i.e. *Rosa* sp.) (Figure S2). Also, the probability of *Q. ilex* seedlings occurrence increased with total shrub volume or the volume of certain shrub families (e.g. *Asteraceae, Cistaceae, Thymelaeaceae*) up to a threshold, then decreased. This suggests that under water-limited conditions, shrubs could aggravate summer water stress shifting from facilitation to competition, especially at high cover (Maestre et al., 2009). For *Leguminosae* shrubs, which marginally increased with the probability of occurrence of *Q. ilex* seedlings in planted forests, it is possible that the denser and more homogeneous tree layer in planted than in secondary forests diminishes their competitive ability (Martín-Alcón et al., 2015) while their facilitative characteristics (e.g., atmospheric N fixing, herbivore protection) persist.

Some species in the *Cistaceae* family can inhibit competitors by allelopathy (Araniti et al., 2012; Chaves et al., 2001) and its highly competitive behaviour, which is in consonance with the drastic drop in the probability of seedlings occurrence for *Q. ilex* with high volumes of *Cistaceae*. Rolo et al., (2013) showed lower facilitative capacity of *Cistus ladanifer* on *Q. ilex* seedlings compared to the leguminous shrub *Retama sphaerocarpa* mediated by lower soil humidity under *C. ladanifer*. We know little about the mechanisms behind the similar patterns found for *Thymelaeaceae* and *Asteraceae* shrubs and *Q. ilex* seedlings in the Mediterranean context (but see references compiled in Table S2) and future research should be done to unravel facilitative or competitive mechanisms. The main species of *Thymelaeaceae, and Asteraceae* in the study area shared a functional space related to relatively short height and being evergreen but other traits related to facilitation ability were contrasting (Figure S2).

5. Conclusions for forest management

Our study shows that the relationships between shrub abundance and tree recruitment are complex and vary with forest type, the interacting species, and the ontogeny of tree recruits (seedlings and juveniles). The fact that contrasting shrub families had a differential effect on tree recruitment can be used in forest restoration projects aiming to optimise regeneration through tree and shrub cover management. This can be specially relevant for pines whose recruitment is low. Species spatial distribution may not only be the result from biotic interaction but from differences in habitat preferences or dispersal capacity (Chacón-Labella et al., 2017; Hart et al., 2017; McIntire and Fajardo, 2009). Because of that, further research would need to be oriented to the mechanisms behind the reported patterns of common shrub families and the recruitment of main tree species in Mediterranean forests.

Overall, secondary forests had higher tree recruitment than planted forests, and planted forests modified the relationships between shrubs and tree recruitment. Therefore, secondary forests originating from old-fields could overall improve tree recruitment, but planting trees coupled with shrub management could further improve tree recruitment. If establishing dense vegetation is not a major restoration goal (e.g., to prevent soil erosion; Mongil-Manso et al., 2016), species other than pioneer pines could be planted as low to moderate shrub cover could enhance future tree recruitment and accelerate forest succession (Cruz-Alonso et al., 2020). Based on our results, average planted forests having 22 m^2 ha^{-1} of basal area in the study area would maximize seedling occurrence with ~236 m^3 of leguminous, and *Quercus ilex* seedling could be maximized in planted forests with 15 m^2 ha^{-1} and ~133 m^3 of leguminous.

Shrub volume could be managed by (1) directly planting or removal during the initial restoration works and/or during the stand management operations (e.g., Prévosto and Ripert, 2008), or (2) thinning the tree overstory to promote understorey species (Battles et al., 2001). These recommendations can complement other practices such as planting trees close to the canopy of pre-existing nurse-shrub species (Gómez-Aparicio et al., 2004; Rey et al., 2009).

CRediT authorship contribution statement

Enrique Andivia: Writing – review & editing, Methodology, Conceptualization. **Paloma Ruiz-Benito:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Verónica Cruz-Alonso:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Pedro Villar-Salvador:** Writing – review & editing, Methodology, Conceptualization. **José María Rey-Benayas:** Writing – review & editing, Methodology, Conceptualization.

Author contributions

All authors conceptualized the idea, defined methodology and contributed substantially to the writing of the manuscript. PRB and VCA curated the data. VCA analysed the data, visualized results and wrote the original draft of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123199.

Data availability

I have shared my data at the "Attach Files" step

Tree recruitment and shrub abundance in planted and secondary forests (Figshare)

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